

AN ANALYSIS OF GEOGRAPHICAL VARIATION IN WESTERN NORTH AMERICAN MENZIESIA (ERICACEAE)

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The boreal shrub genus *Menziesia* J. E. Smith consists of four species in Japan and two rather closely related species in North America, one occupying the Appalachian region and the other, *M. ferruginea* Smith (1791), occupying coastal and mountainous areas throughout the moist regions of western North America. All members of the genus are found in mesic habitats. Occasionally they constitute the dominant understory vegetation, especially in coastal bogs and forests and at lake margins in areas of high rainfall or persistent fog or mist.

The western populations were originally described as two separate species. *M. ferruginea* Smith included the coastal populations, and *M. glabella* Gray (1878), a less pubescent and glandular form, occurred in the Rocky Mountains. Intermediate specimens, subsequently collected in the Cascade Range, led Peck (1941) to consider the Cascade and Rocky Mountain plants together as *M. ferruginea* var. *glabella* (Gray) Peck. Calder and Taylor (1965) have recently made the combination *M. ferruginea* ssp. *glabella*.

The pubescence characters used to differentiate the two entities lack the geographical coherence suggested by the proposed systems of classification. The purpose of this study is to examine more carefully and discuss the geographical differentiation within *M. ferruginea*.

METHODS

A total of 143 herbarium specimens was studied from throughout the range of the species. In so far as can be determined, each represents a distinct population. The geographical range of the species has been divided into seven areas on the basis of physiography, climate, geology and political boundaries (Detling, 1948). The areas are: 1, the Alaskan coast; 2, the Canadian coast; 3, the United States coast from Washington to northern California; 4, the northern Cascade Mountains from British Columbia to the Columbia River; 5, the southern Cascade Mountains of Oregon; 6, the Canadian Rocky Mountains; and 7, the Rocky Mountains of the United States as far south as Wyoming. The localities and areas are shown in Fig. 1.

The only well-defined geographical discontinuity between areas occurs in central British Columbia. It isolates the Rocky Mountain populations from all others. The coastal areas are essentially continuous from northern California to the Kenai Peninsula and merge with the Cascade areas through the Manning Park-Mt. Seymour area in southwestern British Columbia. In this instance the line between areas was drawn on geological grounds, keeping the volcanic Cascades as an entity.

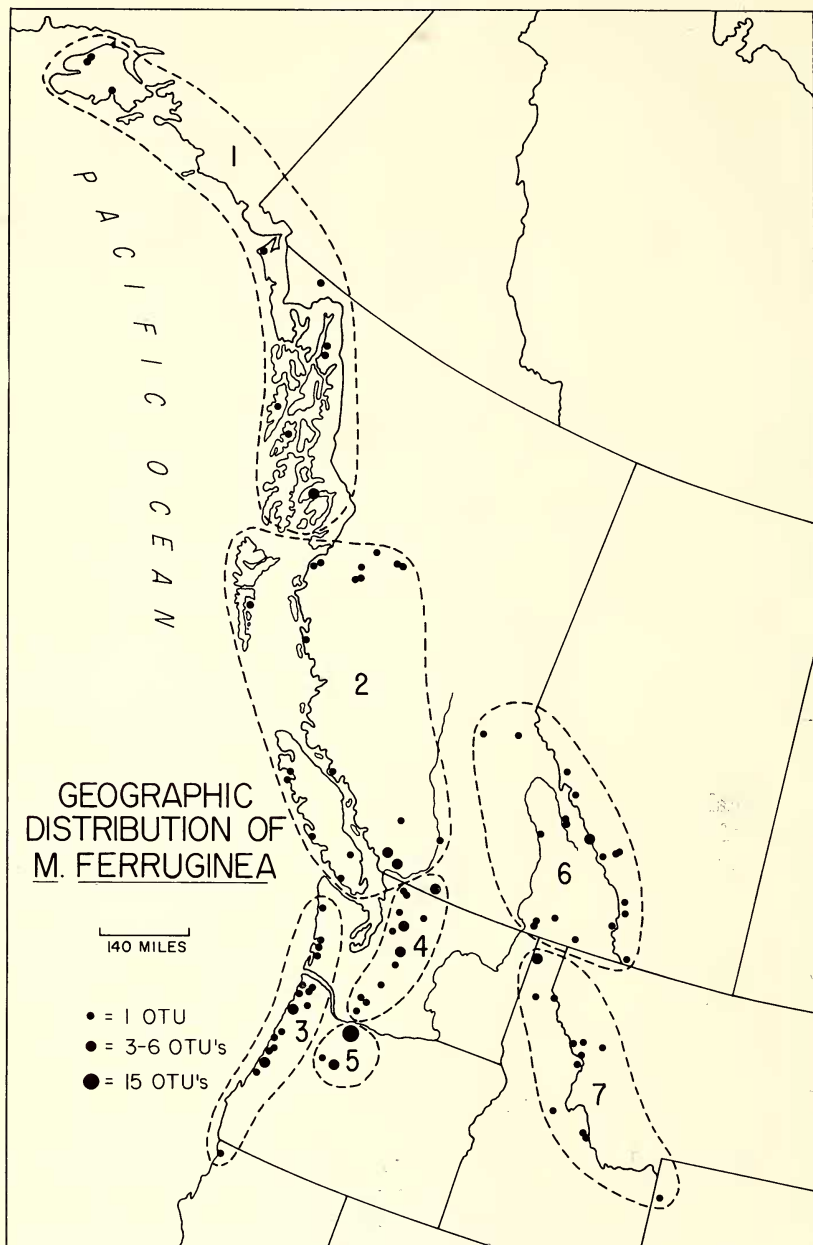


FIG. 1. The localities of analyzed specimens and the boundaries of the geographical sample areas: 1, Alaskan coast; 2, Canadian coast; 3, United States coast; 4, northern Cascade Mountains; 5, southern Cascade Mountains; 6, Canadian Rocky Mountains; 7, United States Rocky Mountains.

Twenty-nine characters were measured. They included leaf tip shape and density and length of glandular and puberulent hairs on the young stem, pedicel, calyx and carpels. For both the upper and lower leaf surfaces, density and length of subulate, glandular and puberulent hairs were measured. Two other characters were derived by summing the densities of subulate and glandular hairs for both surfaces, giving a measure of total leaf pubescence. All leaf density measurements for subulate and glandular hairs were made by superimposing a grid over the leaf surface and counting all those hairs that fell completely within the grid, as well as those along two adjacent sides which had their points of attachment within the grid. Densities of hairs on stems and petioles were measured by counting the number of hair bases visible on a 1 mm segment taken immediately proximal to the oldest leaf, and 1 mm below the calyx, respectively. The puberulent hairs were too small to be counted by these methods, and their densities were approximated by measuring the distance of several hairs to their nearest neighbors. The average distance was then converted to a density measurement. All measurements of length were made with a micrometer. The leaf tip shape index resulted from numerically grading a minimum of ten leaves per specimen from round (1) to acuminate (8).

Sokal and Sneath (1963) suggest using no fewer than sixty characters in numerical taxonomic studies. However, this study concerns subspecific variation, necessitating analysis of a large number of individuals, and the number of characters consequently had to be sacrificed. Ehrlich and Ehrlich (1967) have shown that classifications of butterflies based on small subsets of characters are highly and significantly correlated with the classification based on the total characters sampled. This has also been demonstrated in plants by Johnson and Holm (1968). Although sufficient data are not available to generalize this phenomenon, we might accordingly expect the narrow character set we have chosen to significantly approximate the total variation pattern in *M. ferruginea*.

The variation in each character was analyzed by comparing the means for that character in all paired combinations among the seven areas using analysis of variance (F tests). Multivariate analysis was made following the methodology of Sokal and Sneath (1963). Each herbarium specimen was taken as an operational taxonomic unit and compared with every other OTU to construct two matrices of similarity measures between the OTU's. Taxonomic distance and product moment correlation coefficients were the similarity measures employed. All characters were standardized such that the mean for each is zero with a variance of one. Each matrix was clustered using the unweighted pair-group method with arithmetic means. A phenogram was constructed from each cluster analysis.

RESULTS

For all characters measured, the variation within any one geographi-

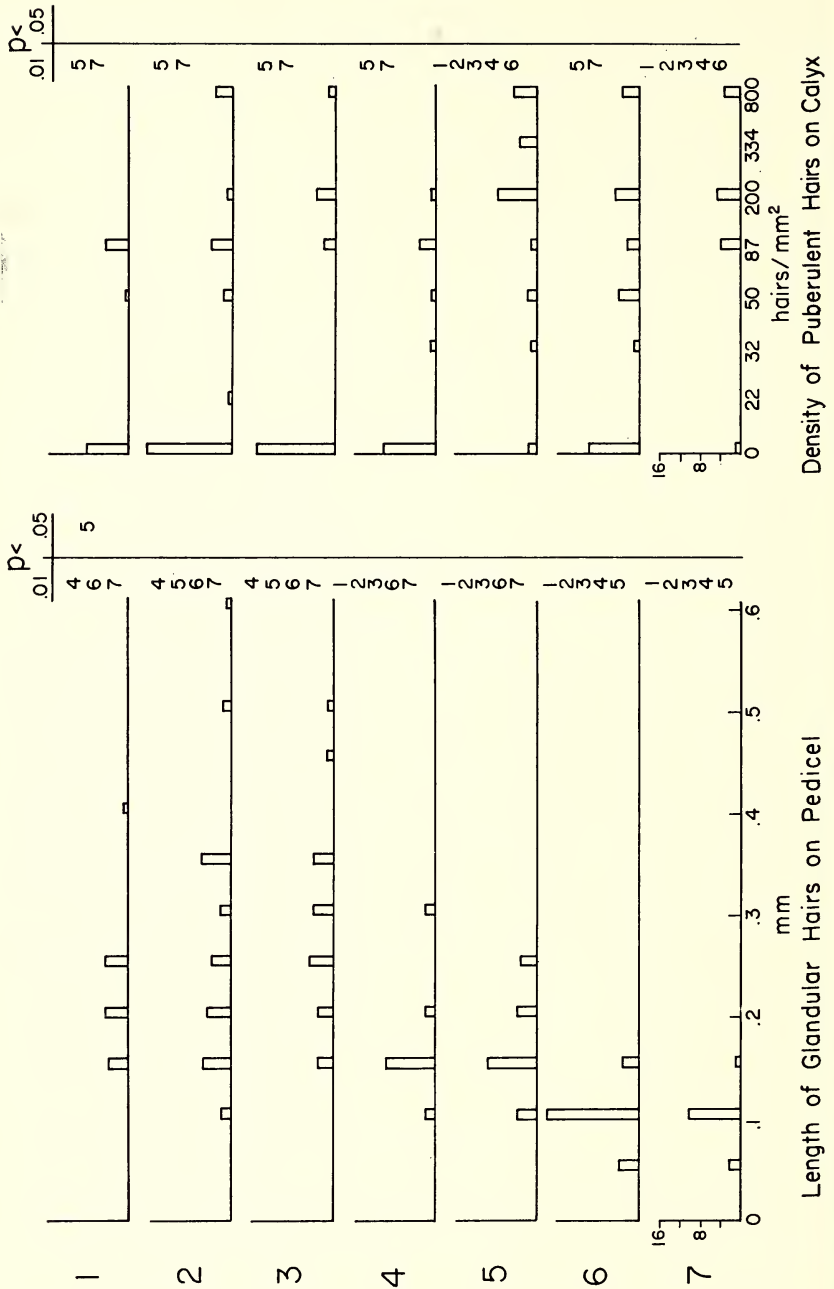


FIG. 2. Character state distributions for four characters for the seven areas (fig. 1). To the right of each histogram are given all areas which differ significantly for that character at the five and one percent levels based on the F test.

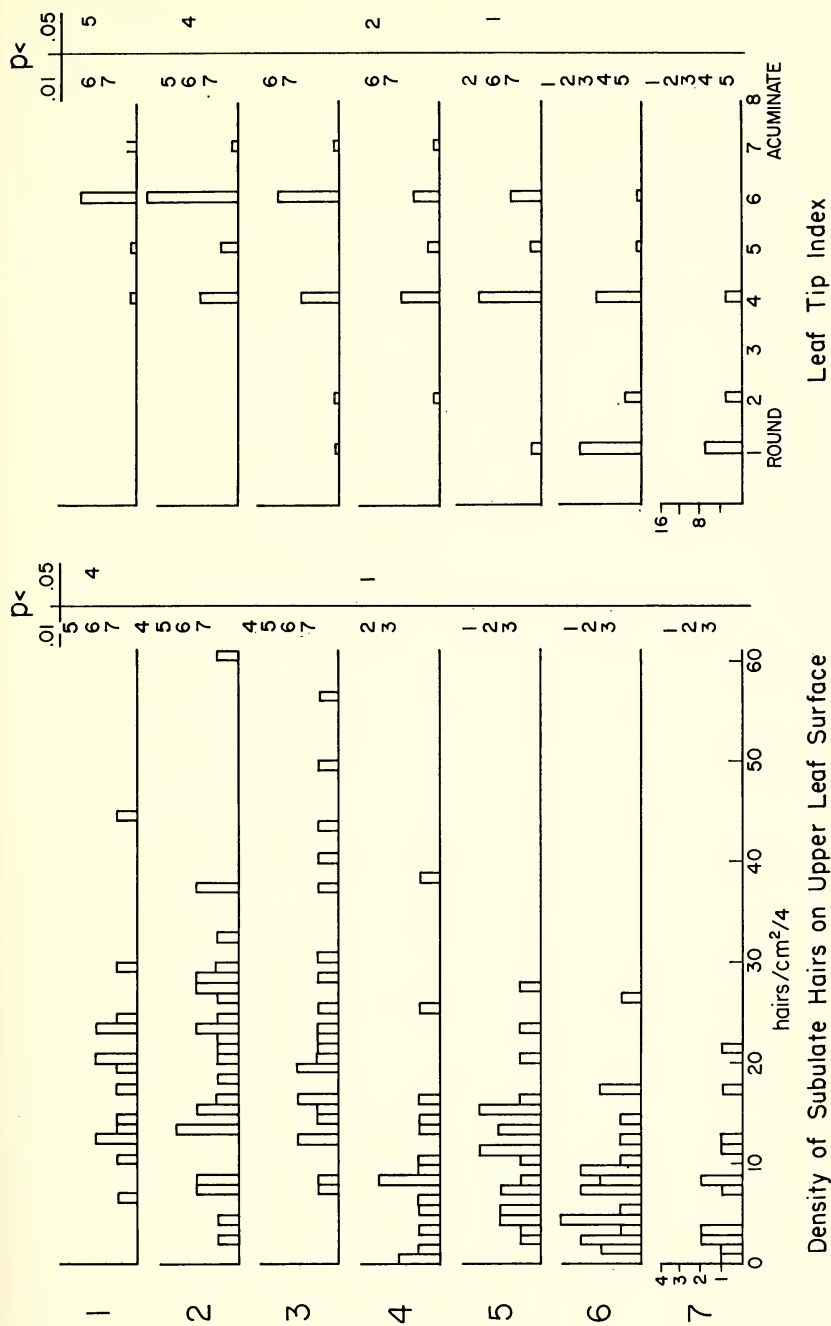


Fig. 2 continued.

TABLE I. A LIST OF THOSE CHARACTERS FOR WHICH THERE ARE NUMEROUS SIGNIFICANT DIFFERENCES BETWEEN GEOGRAPHICAL AREAS IN PAIRED COMBINATIONS. ALSO GIVEN ARE THE GENERAL GEOGRAPHICAL PATTERNS OF VARIATION OF THESE CHARACTERS.

<i>Character</i>	<i>Description of Variation Pattern</i>
Density of subulate hairs on upper leaf surface	Decreasing clinally inland; Cascade and Rocky Mountains similar (fig. 2)
Total density of hairs on upper leaf surface	Decreasing clinally south and inland, but reversed in the Rocky Mountains
Length of subulate hairs on upper leaf surface	Decreasing clinally south and inland
Length of glandular hairs on upper leaf surface	Decreasing clinally south and inland
Density of glandular hairs on lower leaf surface	Decreasing clinally south and inland, but reversed in the Rocky Mountains
Length of glandular hairs on lower leaf surface	Unclear, generally decreasing south and inland
Density of glandular hairs on young stem	Decreasing clinally south and inland, but reversed in the Rocky Mountains
Length of glandular hairs on young stem	Increasing clinally south on coast, decreasing inland
Density of puberulent hairs on pedicel	Increasing clinally south and inland; southern Cascade and U.S. Rocky Mountains similar
Length of glandular hairs on pedicel	Decreasing clinally inland; three groups: Coast, Cascades and Rocky Mountains (fig. 2)
Density of puberulent hairs on calyx	Two groups, no clinal change: southern Cascades and Rocky Mountains similar (fig. 2)
Length of longest cilium on calyx	Increasing clinally south and inland, but reversed in the Rocky Mountains
Density of puberulent hairs on carpel	Coast constant; others increasing south and inland
Density of glandular hairs on carpel	Coast constant; others increasing south and inland
Length of glandular hairs on carpel	Not clinal: Coast lowest; Cascades highest; Rocky Mountains intermediate
Leaf tip index	Decreasing clinally south and inland; jump down-scale (to roundness) at Rocky Mountains (fig. 2)

cal area overlaps the variation in all other areas. A series of histograms of four characters for each of the seven areas is given in Fig. 2. Also included are code numbers for those areas which differ significantly from the area-character under consideration. Significance at $p < .05$ and $p < .01$ is based on the F test between the means. Those characters which exhibit significant differences between samples in several paired combinations are given in Table I, with descriptions of the patterns of character variation.

For character sets involving size, such as those used in this study, Sokal and Sneath (1963) suggest that a correlation coefficient gives a better measure of similarity than taxonomic distance. As predicted, in the phenogram based on taxonomic distance, several geographically unrelated and morphologically diverse specimens clustered with one another or with the major clusters only at unusually high levels. Since these individuals are extreme for one or more measurements, it seems that the clustering pattern here is adversely affected by characters involving size. For this reason, we consider the phenogram based on correlation coefficients to be the more appropriate measure of similarity, and further discussion will pertain to it.

The OTU's fall into three large clusters which we refer to as Rocky Mountain, Cascade and Coastal (fig. 3). The Rocky Mountain cluster is the most homogeneous: it contains Rocky Mountain OTU's almost exclusively, and almost every Rocky Mountain OTU is included in it. The Cascade and Coastal clusters are heterogeneous. They contain a predominance of OTU's from the areas for which they are named, but also include a significant number of OTU's from other areas. The Cascade and Rocky Mountain clusters show greater affinity to one another than either does to the Coastal cluster.

DISCUSSION

The patterns of variation of characters in Table I show an independence, or "discordance." Regarding the problem of concordance and discordance at subspecific levels, Ehrlich and Holm (1964, p. 166) state that "with discordance predominating, subspecies recognized on the basis of one or a few convenient characters would not be evolutionary units. They would be simply units of convenience for filing specimens."

Figure 2 presents a fraction of the original data and demonstrates some of the more important variation patterns in detail. The density of subulate hairs on the upper leaf surface is the most readily observed character for differentiating the described *M. ferruginea* var. *glabella* (Gray) Peck from the more pubescent typical *M. ferruginea* of coastal regions. This character shows a clinal decrease inland, with the Rocky Mountain and Cascade populations varying as a unit. The coastal populations form another quite distinct statistical unit. This character, taken alone, would indicate that Peck was correct in stating that the var. *glabella* should include both Rocky Mountain and Cascade plants (1941). If we consider leaf tip shape, however, another pattern becomes apparent. The coastal and Cascade specimens show a clinal increase in roundness of the leaf tip as one progresses south and inland. The Rocky Mountain plants show a sharp break from all the other populations, having for the most part quite round leaf tips. This pattern, if taken alone, would lead one to consider the Rocky Mountain form to constitute the most nearly distinct subspecific unit. The length of glandular hairs on the pedicel exhibits yet another pattern of variation. Here all

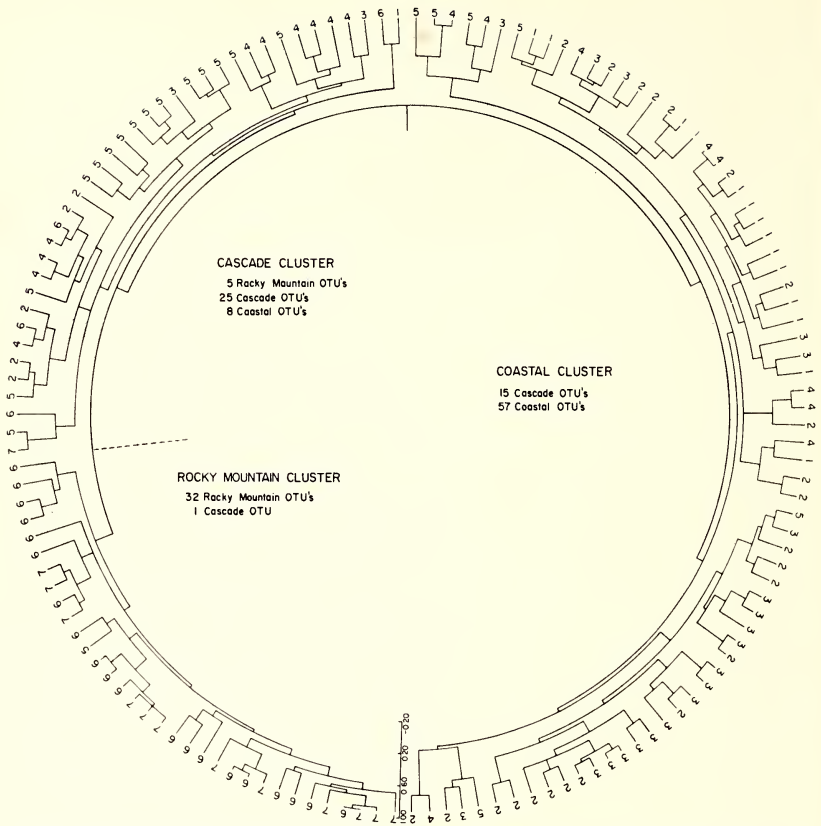


FIG. 3. Phenocycle resulting from the cluster analysis of the matrix of correlation coefficients. The OTU's are labeled as to the geographical area from which they came (fig. 1). A summary of the constituents of each of the major clusters is given. A dotted line marks the boundary between the Cascade and Rocky Mountain clusters.

of the three major groups of populations are significantly different from one another, with the cline again decreasing inland. Although the clines for these three characters are generally similar, their relative expressions follow different patterns, and they must thus be considered discordant characters.

Hitchcock, *et al.* (1959) state the range of *M. ferruginea* var. *glabella* (Gray) Peck as follows: "Rocky Mts., Alta. and B.C. to Wyo., westward to e. Wash. and Oreg. and down the Columbia to Mt. Hood and Mt. Adams, where the two varieties freely interbreed." The only specimen from the Columbia Plateau Province of which we are aware was collected at Twin Lakes, in northeastern Washington (Ferry Co.). This collection came to our attention too late to be included in the analyses. In fact, *Menziesia* seems to be poorly collected throughout the critical

western part of the Rocky Mountain areas. However, some indirect evidence supporting Hitchcock's statement is found by referring to the density of puberulent hairs on the calyx in Fig. 2. The Oregon Cascade and United States Rocky Mountain areas form a single statistical population, separate from all others, being the only areas in which the mode for this character is not zero. The pattern of variation for this character would certainly indicate some degree of gene flow across the Columbia Plateau or the northern Great Basin in the present or recent geologic past.

The foregoing comments necessitate a more detailed consideration of the probable migrational history of the genus in western North America. It appears from present distributions of member species and by analogy with ecologically similar species which have left a paleontological record that *Menziesia* has migrated southward from an originally boreal distribution with the increasingly temperate climate in this region during the first half of the Tertiary. In the Ericaceae, generic distinctions on the basis of pollen morphology are difficult, and direct evidence of *Menziesia's* migrational routes are lacking (Hansen, 1947; 1955; Heusser, 1960). The following discussion assumes that *Menziesia* has a similar migrational history to other boreal species whose pollen records have been studied.

In Wisconsin Pleistocene times, glaciers formed in the mountains of British Columbia, which led to the development of more massive piedmont glaciers and finally to a virtually continuous ice sheet that covered all of western Canada and the northern half of Washington and parts of Idaho and Montana. Alpine valley glaciers and piedmont glaciers also formed in the mountain ranges much farther to the south (Flint, 1945; 1957). The interior of Alaska and the more westerly portions of the Yukon Territory were not covered by the ice sheet. This area must have acted as a refugium for many boreal species during the Wisconsin glacial period. The western North American ice sheet was thickest and persisted the longest in central British Columbia where it had no direct outlets (Flint, 1957); *Menziesia* is today absent from this area. It seems likely that this is due not only to the long persistence of Wisconsin ice, but to the warming and drying trend which immediately followed the melting of the glaciers and culminated about 6,000 years ago (Hansen, 1947; 1955) making the area climatically unsuitable for *Menziesia*.

It also seems likely that during glacial periods *Menziesia* occupied much area in the southern Cascades and the Great Basin where it has not been able to persist. Certain present distributions support this hypothesis. *Menziesia* commonly co-occurs with *Chamaecyparis nootkatensis* (Lamb.) Spach along the coasts of British Columbia and Alaska. The two also co-occur at the southernmost montane locality known for *Menziesia*, in the Oregon Cascades (*J. C. Hickman 492-4, ORE.*; *J. C. Hickman 492-5, ORE.*). Several collections of *Chamaecyparis* have also been taken from an evidently relictual population of

large trees in the Aldrich Mountains of east-central Oregon (*A. Cronquist* 7646, DS; *O. V. Mathews*, 1940 DS). These collections may indicate that cool, moist conditions prevailed during the Pleistocene in much of what is now semi-arid region between the Cascade and Rocky Mountains, and that *Menziesia* could have been widely distributed through this area.

The interrelationships among the populations have also been analyzed by computing phenetic similarity (fig. 3). On the lower clustering levels the complexity of patterns is the most striking characteristic. This is not true for the Rocky Mountain areas, however, indicating that they constitute the least variable grouping. Other small clusters show great geographical diversity in their members: OTU's cluster first with a member of the same area in only one third of the instances. It is the higher clustering levels that should be expected to indicate possible sub-specific taxonomic divisions. The Rocky Mountain populations and the bulk of the Cascade populations cluster in a large group, parallel to the large group of coastal forms with which the remainder of the Cascade individuals are more closely allied. Here the homogeneity of the Rocky Mountain cluster does not imply that these plants constitute the most distinct grouping. It is not surprising that the Cascade and Rocky Mountain materials are phenetically similar since these two areas probably have greater environmental similarities than has either with the coastal area. That the Coastal cluster contains numerous OTU's from the Cascade area (and the converse) suggests the possibility of greater or more recent gene flow between them. This is supported by the present geographical continuity between the coastal and Cascade areas at Manning Park and the possibility of more southerly connections in the recent geologic past as suggested by Detling (1954; 1958).

CONCLUSIONS

The variation pattern in *Menziesia ferruginea* is complex. Univariate and multivariate analyses show that no single character nor set of characters studied can be used to separate individuals into geographically or ecologically coherent categories. Thus, the erection of subspecific taxa is inappropriate and inadequate for describing this pattern. It must rather be explained in terms of migrational history, past and present gene flow, and adaptations to existing environments. These factors have led to an overlapping and partially discordant complex of morphological clines from north to south and from the coast to the Rocky Mountains. We suggest that in future works botanists consider *M. ferruginea* Smith var. *glabella* (Gray) Peck to be a later synonym for *M. ferruginea* Smith.

ACKNOWLEDGMENTS

The authors would like to thank the late L. E. Detling for his advice throughout the course of this work and S. A. Cook for his continuing interest and counsel. Richard W. Holm, Duncan M. Porter and Thomas

A. Ebert kindly read and commented on the manuscript. The materials used in this study came from the following herbaria: DS, OSC, ORE, UBC, WTU, UC, and MICH. We would like to express our gratitude to Adam F. Szczawinski and Marion Ownbey, for their kind cooperation. Computer time for the analysis of variance was provided by the University of Oregon Statistical Laboratory and Computing Center. Multivariate analysis were done at the Stanford University Computer Center using programs modified from NT-SYS developed by F. James Rohlf. The work has been supported in part by Grant 2G-365-R1 from the U.S. Public Health Service-National Institutes of Health to Stanford University.

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